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Woodlice (Isopoda: Oniscidea): their potential for assessing sustainability and use as bioindicators

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Abstract

Those features of the biology of terrestrial isopods which make them appropriate organisms for assessing sustainability are described. They are very widespread, easily identified and form a dominant component of the soil arthropod macrodecomposer community in many temperate habitats, reaching densities of up to 3000 m^{-2} in calcareous grasslands. They feed on dead organic material and are key system regulators of the ecosystem functions of decomposition and nutrient recycling. They can be sampled readily by hand, pitfall trapping or extracted from soil by heat and light. They are sensitive to pesticide applications, marked differences in density being found between conventional and organic cultivation regimes. Isopod biomass is higher under no-tillage or minimum tillage regimes which leave crop residues near the soil surface. Isopods tolerate some heavy metals by accumulating them in vesicles in the hepatopancreas. They are thus, potentially useful for monitoring bio-accumulation of such contaminants and can serve as bioindicators of heavy metal pollution. ©1999 Elsevier Science B.V. All rights reserved.

Keywords: Woodlice; Bioindicators; Terrestrial isopods; Oniscidea; Soil contamination; Heavy metals; Rural landscape; Sustainability

1. Introduction

Woodlice (also called sow bugs, pill bugs and slaters) are terrestrial isopods (class of Crustacea, sub-order Isopoda) of the family Oniscidea, which have invaded terrestrial habitats from aquatic environments. Most species can still tolerate submersion in water saturated with O_2 (Edney, 1968). In fact, some terrestrial isopods, e.g., *Ligidium*, and some specialized cave isopods in the Trichoniscidae, escape into water in pools or hollows when disturbed. In addition, some genera, e.g., *Ligia*, which live in intertidal, littoral environments with hard substrates (rocky shores, dikes, breakwaters), can also tolerate submersion. Other species have colonized very xeric environments, even deserts, by decreasing their permeability to water loss and synchronizing foraging activity to diurnal changes in microclimate (Warburg et al., 1984).

Most members of the sub-order are small to medium sized organisms (1.2–30 mm), with approximately 5000 species distributed worldwide from deserts to forests, rangelands, agroecosystems, up mountains and in subterranean caves. There are several life forms: (1) runners, which have large eyes, long legs, and sometimes mimetic colors; (2) rollers, capable of rolling into a tight ball when disturbed; (3) clingers, less mobile than the preceding forms and with depressed margins of the body which they press down on

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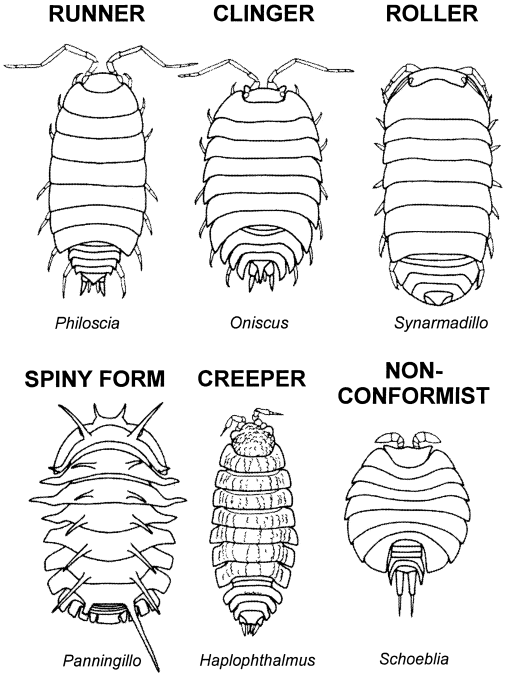

Fig. 1. Some features of terrestrial isopod morphology. Ecomorphological categories are modified from Schmalfuss (1984). Most of the specimens collected by pitfall traps belong to the runner, clinger and roller categories.

flat surfaces, and (4) creepers, which have developed tergal ribs and live in narrow interstices, caves, etc. (Fig. 1) (Schmalfuss, 1984, 1989). The body surface is covered by setae, scales, glands and sometimes ornaments in various shapes (Holdich, 1984). Strategies to improve body impermeability have been developed to colonize terrestrial environments (Edney, 1968; Sutton and Holdich, 1984; Warburg, 1993).

Their diet consists mostly of decaying organic materials such as leaf litter, decayed wood, fungi, and bacterial mats. Much research has been devoted to consumption in woodlands and grasslands, and has shown that weathering of litter with conditioning by micro-organisms improves its palatability to isopods (Hassall and Rushton, 1984; Hassall et al., 1987). They can eat some animals and occasionally predate insect larvae, for instance, in citrus orchards in California, where *Armadillidium vulgare* (Latreille) has been observed feeding on pupae of fruit flies (*Drosophila*; Edney et al., 1974). They can also be cannibalistic (Brereton, 1954). Coprophagy is used to improve their nutrient uptake; especially for the juveniles (Paoletti and Martinelli, 1981; Hassall and Rushton, 1985).

Although most woodlice live in soils and litter layers, some species are arboreal, especially in the tropical rain forests, e.g., some members of the Philosciidae, Armadillidae and Trachelipidae (Paoletti, 1981, 1988a; Adis and Schubart, 1988; Paoletti et al., 1991). In temperate forests some species such as *Philoscia affinis*, *P. muscorum* and *Porcellio scaber* are frequently found in the forest canopy, on tree bark, leaves and branches, not only when the forest floor is inundated or waterlogged (Favretto et al., 1988; Warburg, 1993). Woodlice are found in their highest densities in calcareous grasslands (up to $3000\,\mathrm{m}^{-2}$, Sutton, 1980), some abandoned fields and on waste ground (see Table 1).

Their impact as possible pests in agroecosystems is limited, and the few documented cases are related to synanthropic species. They can affect seedlings in particular situations in which no alternative food is available (Vandel, 1960; Sutton and Coghill, 1979). Some species have been observed in houses containing old woodwork in roofs, ceilings or in cellars. Most applied reference works on isopods refer to some of the most abundant species such as *A. vulgare*, *Armadillo* spp., *P. scaber*, and a few others; in the applied entomological literature their importance as possible seedling predators is often over-emphasized (Sutton and Coghill, 1979). In general, they are beneficial because of their role in enhancing nutrient cycling, by comminution of organic debris and transporting it to moister microsites in the soil. They also transport propagules of bacteria, fungi and vescicular arbuscolar mycorrhizae through soils (Rabatin and Stinner, 1988).

2. Taxonomy

Detailed taxonomy requires careful dissections for many tropical species, many of which remain to be described. Good guides are available for identifying woodlice in most temperate areas, including those of Vandel (1960) for France and part of Europe; Gruner (1966) for Germany; Sutton (1980), Harding and Sutton (1985), Hopkin (1991), and Oliver and Meechan (1993) for Britain; Schmoelzer (1965) for Central Europe; Argano (1979) for Italy (this key for aquatic isopods includes some terrestrial species), and

Table 1
Comparative abundance and species richness of terrestrial isopods in different environments

Environment	Location	Species number	Individuals/m2	Reference
Cultivated fields	The Netherlands	0–3	0–15	M. Berg, pers. commun., 1997
Coniferous forests, dry	The Netherlands	2	2–5	M. Berg, pers. commun., 1997
Deciduous forests, dry	The Netherlands	4	15	M. Berg, pers. commun., 1997
Deciduous forest, wet	The Netherlands	8	150	M. Berg, pers. commun., 1997
Riparian zone (freshwater)	The Netherlands	9	200	M. Berg, pers. commun., 1997
Coastal area	The Netherlands	9	75	M. Berg, pers. commun., 1997
Ditches/Dikes	The Nethernands	10–14	75–150	M. Berg, pers. commun., 1997
Grassland	Elyaqim, Israel	6	0.95–2.05	Hornung, pers. commun., 1997
Oak woodland	Allonim, Israel	7	0.18–0.37	Hornung, pers. commun., 1997
Planted pine forest	Seger, Israel	6	0.91–1.01	Hornung, pers. commun., 1997
Rough grassland	England	3	1580	Sutton, 1980
Dune grasslands	England	3	390–673	Sunderland et al., 1976
Coastal grassland	California, USA	1	538	Paris and Pitelka, 1962
Broadleaf forest	Japan	3	1476	Watanabe, 1980
4 Deciduous woodlands	North Eastern Italy	13[b]	8–592	Paoletti, 1988b
7 Corn monocultures	North Eastern Italy	13[b]	0–109	Paoletti, 1988b
Organic apple orchard	Lagundo (BZ), Italy	5[a]	420	Paoletti et al., 1995
Conventional orchard	Lagundo (BZ), Italy	3[a]	20	Paoletti et al., 1995
Deciduous forest	Lagundo (BZ), Italy	5[a]	200	Paoletti et al., 1995
Rural landscape, field	South Bohemia	1[a]	0.2	Tajovsky, 1991
Rural landscape, fallow	South Bohemia	2[a]	4.6	Tajovsky, 1991
Rural landscape, meadow	South Bohemia	3[a]	3.6	Tajovsky, 1991
Rural landscape, forest	South Bohemia	5[a]	33.1	Tajovsky, 1991
Calcareous grass, heath	England	4	70–700	Hassall and Dangerfield, 1989
Calcareous grass heath	England	3	60–1000	Hassall and Dangerfield, 1989

[a] Handsorting.
[b] Handsorting and modified Tullgren extraction.

Muchmore (1990) for USA; these guides make identification of the commoner species relatively easy. Fig. 2 shows some common species.

Some very common species such as *Trachelipus rathkei* and *A. vulgare* (Fig. 3) are easily found in European rural landscapes. Several *Porcellio* spp. and *Oniscus asellus* are more common in northern Europe; for instance, in Britain, *O. asellus* and *P. scaber* are the commonest species (Harding and Sutton, 1985), and in The Netherlands *O. asellus*, *P. scaber*, *A. vulgare*, *T. rathkei* and *P. muscorum* are the commonest species (Berg, 1996). This paper follows the family names proposed by Holdich et al. (1984).

3. Collection, sampling and preservation

Direct sampling with forceps or an aspirator is time consuming but sometimes is very effective for collecting different morphological types of woodlice. When comparing different sites the time dedicated to each site must be similar. The use of quadrates (e.g. 40 cm × 40 cm) from which litter and soil are collected and then examined carefully is a modification of direct sampling useful for generating approximate indices of abundance. Litter and soil samples can be extracted using a Berlese–Tullgren apparatus or in a high gradient extractor (Hassall et al., 1988). Soil cores from 6 to 20 cm in diameter, extracted using heat and light gradients, give more accurate density estimates of isopods, including some very small soil dwelling species within the Trichoniscidae and Haplophthalminae in most European and North American regions, and Philosciidae, Platyarthridae, Trachelipidae, etc. in the tropics. Isopods have highly aggregated dispersion patterns (Hornung and Warburg, 1995a, 1995b) so large numbers of replicate samples are required to obtain meaningful estimates of density.

Passive trapping systems are less labor intensive and can be used to compare different environments, bearing in mind the limitations discussed by Topping and Sunderland (1992). Pitfall traps can give an index of

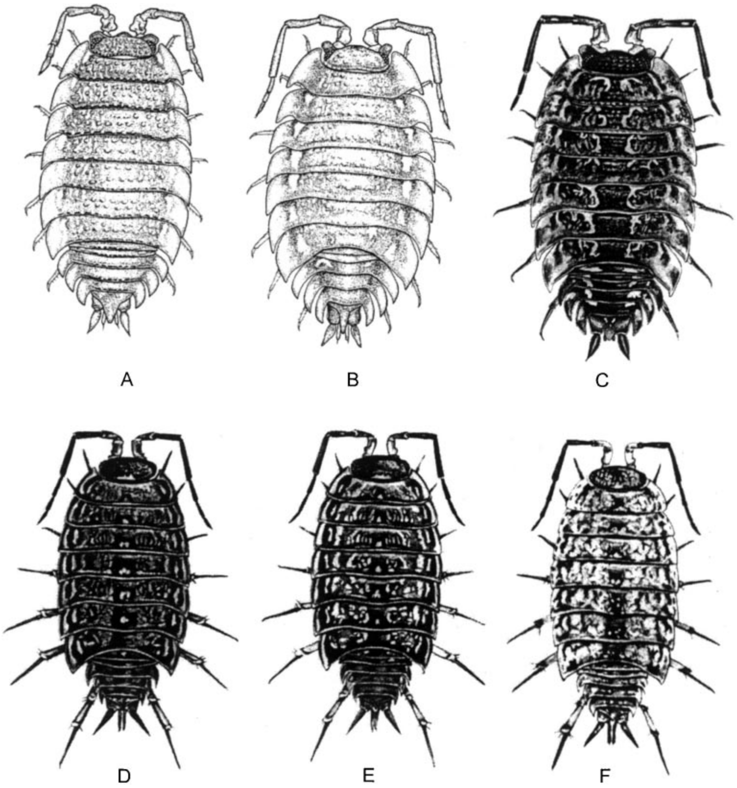

Fig. 2. Some key species that are common in Europe and extensively used to monitor disturbed landscapes (modified from Sutton et al., 1972). A: *P. scaber*, length 12 mm; B: *O. asellus*, length 13 mm; C: *Porcellio* spinicornis; D, E, F: different color patterns of *P. muscorum*, length 6–8 mm.

the activity/density of isopods living and moving at the soil surface, but interpretation of results is difficult because of the inability to distinguish between variations in activity and abundance in different habitats or seasons. Isopods that live in the soil like *Androniscus* spp. and *Haplophthalmus* spp. are not adequately sampled using this method. Traps can contain preservatives such as an aqueous solution of 40% ethylene glycol plus a drop of detergent or preferably propylene glycol, which is more safe and atoxic but more expensive. Ten to twenty traps per site are sufficient to compare different fields or sites of a landscape. A solution of 70–80% ethyl alcohol +2% glycerol is a good preservative for long term storage.

4. Distribution

Among the 42 species of woodlice living in Britain, at least 13 are considered non-native and accidentally introduced by man (Sutton et al., 1972; Sutton and Harding, 1989). In the Netherlands 36 species have been listed, seven of which live only in hot greenhouses and are, therefore, non-native (Berg, 1996). Approximately 650 species have been described in central and southern Europe (Schmoelzer, 1965), and about 360 species live in Italy (F. Ferrara, pers. commun.). Because of their requirement for calcium in their exoskeletons, isopods are usually more abundant in calcareous than acid soils.

5. Predators and parasites

An array of different animals prey upon isopods, including vertebrates such as birds, frogs, lizards, mammals (particularly shrews) and invertebrates, including spiders such as *Dysdera crocata*, some scorpions, chilopods, ground beetles, and other polyphagous

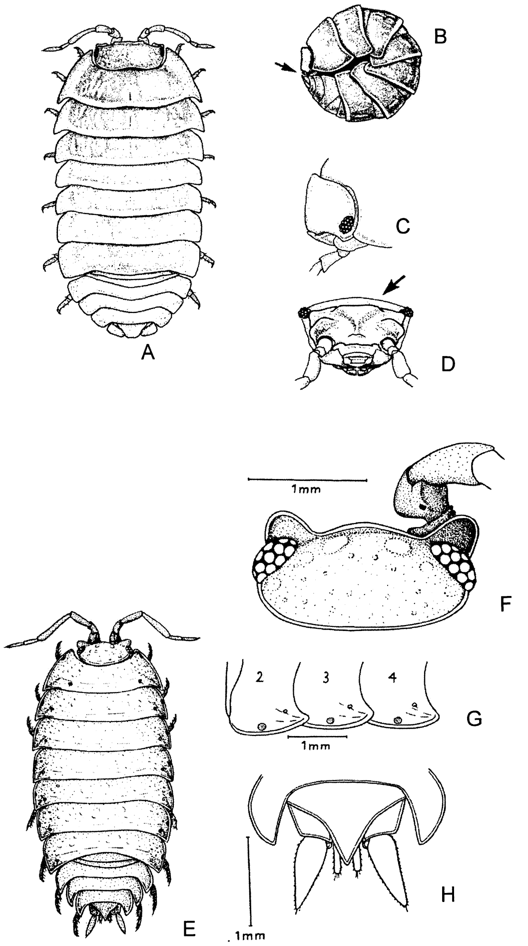

Fig. 3. *A. vulgare* (A–D). A: dorsal view of a moving specimen; B: lateral view of the rolled-up specimen, 5-7 mm in diameter; C, D: head, lateral and frontal view, respectively. *T. rathkei* (E–H); E: dorsal view, length 10–12 mm; F: head; G: Lateral view of the pereionites; H: dorsal view of telson and uropods.

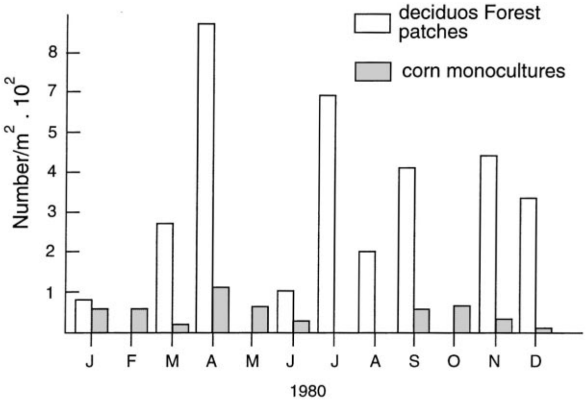

Fig. 4. Mean monthly density of isopods in deciduous woodlands patches in lowlands of north-eastern Italy and in nearby corn monocultures (from 30 cm × 30 cm litter quadrats and 10 cm × 10 cm soil cores extracted with a modified Tullgren funnel). Differences among four woodlands (in different locations) and seven farms were statistically significant. In both corn fields and woodlands the total number of species was 13. The mean number of species per woodland (8) was in general higher than in the farmland (4) (Paoletti, 1987, 1988b).

insects (Sunderland and Sutton, 1980; Warburg et al., 1984; Harding and Sutton, 1985). Several parasites affect isopods, including Tachinid flies, mermithid nematodes, rickettsias and viruses, especially the common iridioviruses, which confer an iridescent blue color to the body of the infected woodlouse (Provenzano, 1983; Federici, 1984).

6. Assessing landscape sustainability

Some researchers have used isopods to assess landscape quality (Paoletti, 1987, 1988b; Jones and Hopkin,1996; Paoletti et al., 1993) but much more work is needed to improve the knowledge about their reliability as indicators compared with other members of the soil biota such as earthworms and carabids. Isopods tend to be more abundant in semi-natural grasslands than woodlands (Davis and Sutton, 1978), but they are more abundant in woodlands than in cultivated habitats (Fig. 4 and Table 1). In general there is a consistent difference in species composition between deciduous woodlands and cultivated areas. For instance, *T. rathkei*, a very common species in rural environments is almost absent from deciduous forest relicts in northeastern Italy, where it has been replaced by other species such as *Lepidoniscus minutus* and *Protracheoniscus* spp. Simlarly, *T. razzautii*, which is normally present near hedgerows and in pastures, is absent from crop fields (Paoletti, 1988a).

Terrestrial isopod diversity decreases rapidly in intensively managed agricultural and sylvicultural landscapes because of a combination of direct and indirect effects of management practices. Direct effects on mortality rates result from application of pesticides, not only of insecticides but also herbicides (Eijsackers, 1981; Farkas et al., 1996; Fischer et al., 1997). Herbicides also have an indirect effect by reducing growth rates and fecundity, as they

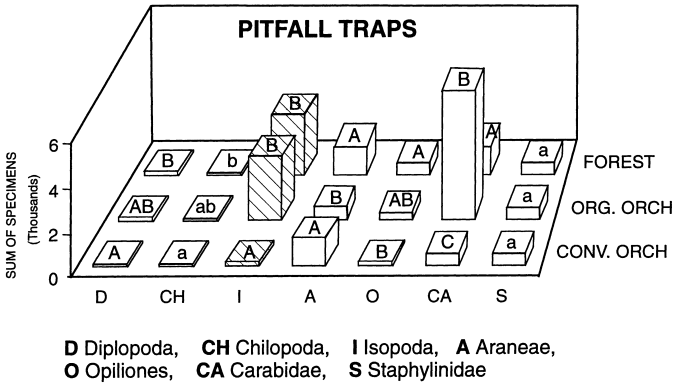

Fig. 5. Pitfall trap data indicating activity/relative density of isopods in an organic apple orchard, conventional apple orchard and a deciduous forest sampled for 1 year. The conventional orchard with higher input had significantly lower isopod activity (different letters: differ with $p < 0.01$) (Paoletti et al., 1995).

reduce availability of high quality food from leaf litter of dicotyledonous plants, which constitute the majority of weeds. Fig. 5 presents a comparison of woodlice found in organic and conventional apple orchards in a fruit-growing region in northern Italy (Paoletti et al., 1995), and Fig. 6 presents a similar analysis of peach orchards in Emiglia Romagna, Italy. These farming systems can be differentiated by the numbers of species present and their total abundance, reduced input practices favoring woodlice. Differences in both biomass and species richness of isopods can therefore indicate the extent of anthropogenic impact in rural areas (Paoletti et al., 1993).

Direct effects on mortality also result from simplification of habitat structure and reduced availability of shelter sites (Hassall, 1996), as occurs with many conventional tillage practices, which also indirectly influence growth and fecundity by burying plant residues.

Reduced tillage operations such as minimum and no tillage, which limit impacts on the soil structure and living crop residues near the soil surface, result in an increase in the biomass of invertebrates, in particular isopods, compared with conventional tillage (Paoletti, 1987; Stinner and House, 1990). In a 6-year study in Bohemia, Tajovsky (1991) observed almost no isopods in some traditionally cultivated fields (rotation of wheat, potatoes, barley) compared with meadows and forest sites. A low density of isopods was noted only in the 6th year of an alternative organic regime of oats, peas and clover.

7. Heavy metals

Isopods generally respond quickly to environmental contamination and impact, with increased mortality, loss of biomass and a decrease in the number of species, resulting from heavy levels of pollution (Paoletti et al., 1993; Jones and Hopkin, 1996). Isopods can accumulate high levels of heavy metals, especially copper (Wieser et al., 1977; Hopkin and Martin, 1984; Paoletti et al., 1988; Hopkin et al., 1989). Besides copper, other heavy metals such as zinc, lead and cadmium are accumulated in vesicles such as lysosomes (Prosi and Dallinger, 1988). Because they adopt a tolerance strategy of immobilizing and accumulating heavy metals rather than preventing absorption or increasing efficiency of excretion, isopods act as bioaccumulators of these pollutants. As they are also large, conspicuous and very easily collected, they are well suited to act as bioindicators of heavy metal contamination in saprophagous food chains (Hopkin et al., 1986, 1989, 1993; Paoletti et al., 1988, 1996; Dallinger et al., 1992; Farkas et al., 1996). Isopods have been convincingly useful for monitoring heavy metal pollution in industrialized and urbanized areas (Paoletti et al., 1988; Dallinger et al., 1992).

Since they are also predated by a wide range of other invertebrates and vertebrates, their bioaccumulation of toxic materials can also have ramifications for trophic levels higher up the food chain.

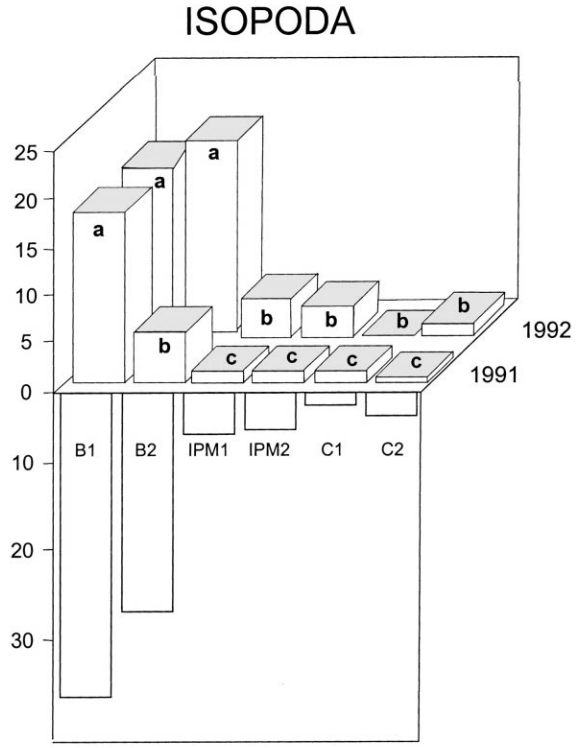

Fig. 6. Pitfall trap data indicating activity/density of isopods in different input peach farms in Emilia Romagna, Italy, sampled over 2 years. In both the years there was a significant difference between the two biological farms and all the other integrated and conventional (high input) farms. The different letters represent statistically different numbers ($p < 0.05$). The lower part of the graph represents the sum of activity/relative density over 2 years (Paoletti et al., 1993, 1996). B1 and B2 = organic peach orchards; IPM1 = integrated peach orchard with a spontaneous cover vegetation; IPM2 = integrated peach orchard with soil tillage to eliminate weeds; C1, C2 = conventional, high input orchards.

8. Conclusions

Terrestrial isopods are abundant and widespread members of the soil macrofauna whose basic biology is now well understood. In temperate regions they are often the dominant component of the arthropod macrodecomposer guild and serve as key system regulators for the ecosystem functions of decomposition and nutrient recycling in some habitats. Because they are sensitive to tillage, changes in litter input, application of pesticides and other contaminations, comparing their abundance on sites subjected to different management regimes can give insight into how changes in land management can affect ecosystem functioning. As isopods tolerate high levels of some heavy metals by accumulating them in their hepatopancreas they can also potentially be used as bioindicators in assessing levels of heavy metal contamination.

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References

Adis, J., Schubart, H.O.R., 1988. Ecological research on arthropods in central Amazonian forest ecosystems with recommendations for study procedures. In: Cooley, J.H., Golley, F.B. (Eds.), Trends in Ecological Research for the 1980 NATO Conference Series. Plenum Press, New York, pp 111–144.

Argano, R. 1979. Isopodi. Consiglio Nazionale delle Ricerche, Roma, p. 65.

Berg, M.P., 1996. Preliminary atlas of the terrestrial isopods of The Netherlands. Report D95006, Department of Ecology and Ecotoxicology, Vrije University, Amsterdam, p. 56.

Brereton, J. Le, G., 1954. A study of factors controlling the population density of some terrestrial isopods. D.Phil. Thesis, University of Oxford, unpublished.

Dallinger, R., Berger, B., Birkel, S., 1992. Terrestrial isopods: useful bioindicators of urban metal pollution. Oecologia 89 (1), 32–41.

Davis, R.C., Sutton, S.L., 1978. A comparative study of changes in biomass of isopods inhabiting dune grassland, Sci. Proc. R. Dubl. Soc. Ser. A, 6, 223–233.

Edney, E.B., 1968. Transition from water to land in isopod crustaceans. Am. Zoologist 8, 309–326.

Edney, E.B., Allen, W., McFarlane, J., 1974. Predation by terrestrial isopods. Ecology 55, 428–433.

Eijsackers, H., 1981. Assessment of toxic effects of the herbicide 2.4.5-T on the soil fauna by laboratory tests. In: Dindal, D.L. (Ed.), Soil Biology As Related to Land Use Practices. Office of Pesticide and Toxic Substances, EPA, Washington, DC, pp. 427–440.

Farkas, S., Hornung, E., Fischer, E., 1996. Toxicity of copper to *Procellio scaber* Latr. Isopoda under different nutritional status. Bull. Environ. Contam. Toxicol. 57, 582–588.

Favretto, M.R., Paoletti, M.G., Lorenzoni, G.G., Dioli, E., 1988. Lo scambio di invertebrati tra un relitto di bosco planiziale ed agroecosistemi contigui. L'artropodofauna del bosco di Lison. Nova Thalassia, pp. 329–358.

Federici, B.A., 1984. Diseases of terrestrial isopods. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods.

The Zoological Society of London. Clarendon Press, Oxford, pp. 233–244.

Fischer, E., Farkas, S., Hornung, E., Past, T., 1997. Subletal effects of an Organophosphorus insectiside, dimethoate, on the Isopod *Porcellio scaber* Lat.. Comp. Biochem. Physiol. 116 (2), 161–166.

Gruner, H.E., 1966. Die Tierwelt Deutschlands: Krebstiere order Crustacea. 5, Isopoda Fisher Jena 2, 151–380.

Harding, P.T., Sutton, S.L., 1985. Woodlice in Britain and Ireland: Distribution and habitat. Institute of Terrestrial Ecology, Huntingdon, p. 151.

Hassall, M., 1996. Spatial variation in favorability of a grass heath as a habitat for woodlice (Isopoda: Oniscidea). Pedobiologia 40, 514–528.

Hassall, M., Dangerfield, J.M., 1989. Inter-specific competition and the relative abundance of grassland isopods. Monitore Zool. Ital. n.s. 4, 379–397.

Hassall, M., Dangerfield, J.M., Manning, T.P., Robinson, F.G., 1988. A modified high-gradient extraction for multiple samples of soil macro-arthropods. Pedobiologia 32, 21–30.

Hassall, M. and Rushton, S.P., 1984. Feeding behaviour of terrestrial isopods in relation to plant defence and microbial activity. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. The Zoological Society of London. Clarendon Press, Oxford, pp. 487–505.

Hassall, M., Rushton, S.P., 1985. The adaptive significance of coprophagous behaviour in the terrestrial isopod *Porcellio scaber*. Pedobiologia 28, 169–175.

Hassall, M.P., Turner, T.G., Rands, M.R.W., 1987. Effects of terrestrial isopods on the decomposition of woodland leaf litter. Oecologia 72, 597–604.

Holdich, D.M., 1984. The cuticular surface of woodlice: a search for receptors. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. The Zoological Society of London. Clarendon Press, Oxford, pp. 9–48.

Holdich, D.M., Lincoln, R.J., Ellis, J.P., 1984. The biology of terrestrial isopods: terminology and classification. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. The Zoological Society of London. Clarendon Press, Oxford, pp. 1–6.

Hopkin, S.P., 1991. A key to the woodlice of Britain and Ireland. Field Studies 7, 599–650.

Hopkin, S.P., Martin, M.H., 1984. Heavy metals in woodlice. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. The Zoological Society of London. Clarendon Press, Oxford, pp.143–166.

Hopkin, S.P., Hames, C.A.C., Bragg, S., 1989. Terrestrial isopods as biological indicators of zinc pollution in the Reading area, south-east England. In: Ferrara, F., Argano, R., Manicastri, C., Schmalfus, H., Taiti, S. (Eds.), Proceedings of the Second Symposium on the Biology of Terrestrial Isopods, Monitore Zoologico Italiano (4): 477–488.

Hopkin, S.P., Hardisty, G., Martin, M.H., 1986. The woodlouse *Porcellio scaber* as a biological indicator of zinc, cadmium, lead, lead and copper pollution. Environ. Pollution 11, 271–290.

Hopkin, S.P., Jones, D.Y., Dietrich, D., 1993. The isopod *Porcellio scaber* as a monitor of the bioavailability of metals in terrestrial ecosystems: towards a global woodlouse watch scheme. Sci. Total Environ. 1993 (S), 357–365.

Hornung, E., Warburg, M.R., 1995a. Seasonal changes in the distribution and abundance of isopod species in different habitats within the Mediterranean region of northern Israel. Acta Oecologica 16 (4), 431–445.

Hornung, E., Warburg, M.R., 1995b. Isopod distribution at different scaling levels, Crustacean Issues 9, (Balkema Publ.), pp. 83–95.

Jones, D.T., Hopkin, S.P., 1996. Reproductive allocation in the terrestrial isopods *Porcellio scaber* and *Oniscus asellus* in a metal-polluted environment. Functional Ecol. 10, 741–750.

Muchmore, W.B., 1990. Terrestrial isopoda. In: D. L. Dindal, Soil Biology Guide. Wiley NY, pp. 805–817.

Oliver, P.G., Meechan, C.J., 1993. Woodlice. Synopsis of the British Fauna (New Series), Field Studies. vol. 49, The Linnean Society, London, pp. 135.

Paoletti, M.G., 1981. Le strategie di vita nella foresta tropicale: interesse teorico ed applicativo anche per gli ecosistemi delle regioni temperate. Il paradosso della fauna pensile del suolo. Natura e Montagna, Bologna, 28, 115–128.

Paoletti, M.G., 1987. Terrestrial isopods in the agroecosystems of the low-lying plain in North-eastern Italy. In: Striganova, B.R.(Ed), Soil Fauna and Soil Fertility. Proc. 9th. Int. Coll. Soil Zoology, Moscow Nauka, pp. 423–426.

Paoletti, M.G., 1988a. Life strategies of isopods and ’soil invertebrates’ in Venezuela. Proceedings of the Second Symposium on the Biology of Terrestrial Isopods. Monograph ser. Mon. Zool. It. 4, 435–453.

Paoletti, M.G., 1988b. Soil invertebrates in cultivated and uncultivated soils in north-east Italy. Redia 71, 501–563.

Paoletti, M.G., Favretto, M.R., Marchiorato, A., Bressan, M., Babetto, M., 1993. Biodiversità in pescheti forlivesi. In: Paoletti M.G. et al. (Eds.) Biodiversità negli Agroecosistemi. Osservatorio Agroambientale, Centrale Ortofrutticola, Forli, pp. 20–56.

Paoletti, M.G., Martinelli, N., 1981. Comparazione delle preferenze alimentari di tre *Androniscus* su substrati vegetali naturali (Isopoda Trichoniscidae) Mem. de Biospeologie. Moulis 8, 33–37.

Paoletti, M.G., Iovane, E., Cortese, M., 1988. Soil pedofauna bioindicators and heavy metals in five agroecosystems in N.E. Italy. Rev. Ecol. Biol. Sol. 25, 33–58.

Paoletti, M.G., Schweigl, U., Favretto, M.R., 1995. Soil microinvertebrates, heavy metals and organochlorines in low and high input apple orchards and coppiced woodland. Pedobiologia 39, 20–33.

Paoletti M.G., Sommaggio D., Bressan, M., Celano, E., 1996. Can sustainable agriculture practices affect biodiversity in agricultural landscapes? A case study concerning orchards in Italy, Acta Jutlandica 71(2), 241–254.

Paoletti, M.G., Stinner, B.R., Stinner, D., Benzing, D., Taylor, R., 1991. Diversity of soil fauna in the canopy of neotropical rain forest. J. Tropical Ecol. 7, 373–383.

Paris, O.H., Pitelka, F.A., 1962. Population characteristics of the terrestrial isopod *Armadillidium vulgare* in California Grassland. Ecology 43, 229–248.

Prosi, F., Dallinger, R., 1988. Heavy metals in the terrestrial isopod *Porcellio scaber* Latreille. Histochemical and ultrastructural characterization of metal-containing lysosomes. Cell Biol. Toxicol. 4, 81–96.

Provenzano, A.J., 1983. The Biology of Crustacea, 6. Pathobiology. Academic Press, New York.

Rabatin, S.C., Stinner, B.R., 1988. Indirect effects of interactions between VAM fungi and soil-inhabiting invertebrates on plant processes. Agric. Ecosyst. Environ. 24, 135–146.

Schmalfuss, H., 1984. Eco-morphological strategies in terrestrial isopods. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. The Zoological Society of London. Clarendon Press, Oxford, pp. 49–63.

Schmalfuss, H., 1989. Phylogenetics in Oniscoidea. In: Ferrara, F., Argano, R., Manicastri, C., Schmalfus, H,. Taiti, S. (Eds.), Proceedings of the Second Symposium on the Biology of Terrestrial Isopods. Monitore Zoologico Italiano 4, 3–27.

Schmoelzer, K., 1965. Ordnung Isopoda. Akademie Berlin, p. 468.

Stinner, B.R., House, G.J., 1990. Arthropods and other invertebrates in conservation-tillage agriculture. Annu. Rev. Entomol. 35, 299–318.

Sunderland, K.D., Hassall, M., Sutton, S.L., 1976. The poplution dynamics *Philosica muscorum* (Crustacea:Oniscoidea) in a dune grassland ecosystem. J. Anim. Ecol. 45, 487–506.

Sunderland, K.D., Sutton, S.L., 1980. A serological study of arthropod predation in woodlice in a dune grassland ecosystem. J. Anim. Ecol. 49, 987–1004.

Sutton, S.L., 1980. Woodlice. Pergamon Press, Oxford.

Sutton, S.L., Coghill, H., 1979. Woodlice and their control. Leaflet, Ministry of Agriculture, Fisheries and Food, No. 623, 1–6.

Sutton, S.L., Harding, P.T., 1989. Interpretation of the distribution of terrestrial isopods in the British Isles. In: Ferrara, F., Argano, R., Manicastri, C., Schmalfus, H., Taiti, S. (Eds.), Proceedings of the Second Symposium on the Biology of Terrestrial Isopods. Monitore Zool. Ital. 4, 43–61.

Sutton, S.L., Holdich, D.M., 1984. The Biology of Terrestrial Isopods. The Zoological Society of London. Clarendon Press, Oxford, p. 518.

Sutton, S., Harding, P., Burn, D., 1972. Key to British Woodlice. Ginn & Company London, UK, p. 106.

Tajovsky K. 1991. Terrestrial Isopods (Oniscidea) in a secondary successional row and abandoned fields. Proceedings of the 4th ECE/XIII.SIEEC, Godollo, pp. 808–813.

Topping, C.J., Sunderland, K.D., 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. J. Applied Ecol. 29, 485–491.

Vandel, A. 1960–1962. Isopodes Terrestres. Faune de France. Lechevalier, Paris, vol. 64, 66, pp. 416 and 931.

Warburg, M.R., 1993. Evolutionary biology of Land Isopods. Springer, Berlin, p. 159.

Warburg, M.R., Linsenmair, K.E. Bercovitz, K., 1984. The effect of climate on the distribution and abundance of isopods. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. The Zoological Society of London, Clarendon Press, Oxford, pp. 339–367.

Watanabe, H., 1980. A study of the three species of isopods in an aevergreen broad-leaved forest in southwestern Japan. Rev. Ecol. Biol. Sol. 17 (2), 229–239.

Wieser, W., Dallinger, R., Busch, G., 1977. The flow of copper through a terrestrial food chain II. Factor influencing the copper content of isopods. Oecologia 30, 265–272.